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Pollination of *Grewia asiatica* (Malvaceae) by *Megachile cephalotes* (Hymenoptera: Megachilidae): Male vs. Female Pollination

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Abstract

The difference in behavior and morphology of male and female solitary bees-owing to different roles they perform- may alter their pollination effectiveness. The present study was aimed to study the difference in foraging behavior of male and female *Megachile cephalotes* Smith (Megachilidae) and its ultimate impact on pollination efficiency in terms of pollen deposition, fruit setting and post-harvest characters of phalsa crop, *Grewia asiatica* L. (Malvaceae). The effect of different environmental factors (light intensity, temperature, relative humidity and wind velocity) on foraging behavior was also studied. Visitation frequency, visitation rate and pollen deposition of females were significantly higher than that of males. Female individuals had also an edge over male counterparts by having longer body and proboscis lengths. Males continued their activity throughout the day in low abundance without notable fluctuation while females attained their peak at 12:00 pm followed by a gradual decline until 4:00 pm. The maximum average fruit weight was recorded for female *M. cephalotes* pollinated fruits followed by open and male pollinated fruits. The shelf life in terms of post-harvest fruit weight and wrinkling was notably lower and more gradual in female pollinated fruits than open and male pollinated fruits. Our results suggest that female *M. cephalotes* are better pollinators of *G. asiatica* in terms of its reproductive success and post-harvest parameters than the males. Future studies should consider the biology and ecology of *M. cephalotes* with special focus on its artificial nesting.

Introduction

In pollinator-dependent crops, high productivity in terms of quantity and quality of fruit and seed set is the function of good pollination (Burd, 1994). Bee potentially contribute to global food security by improving shape, size and post-harvest features (e.g. shelf life, firmness, color and sugar contents etc.) of many commercially grown fruits and vegetables (Klatt, 2013). The vast majority of pollinator species is wild, including more than 20,000 species of bees (Potts et al., 2016).

The foraging behavior of pollinators (e.g. visitation frequency, visitation rate, seek for pollen and nectar and nectar robbing) can significantly affect pollen deposition on stigma (Ohara & Higashi, 1994; Kudo, 2003). The foraging behavior of female solitary bees is better studied so far. However, some recent studies have shown considerable differences in life history, foraging behavior and ecology of male counterpart of the same species (Neeman et al., 2006; Cane, 2010; Pascarella, 2010). Although both the sexes feed on floral nectar in order to meet their own caloric need, their floral diet may also be as dissimilar as the diet of different bee species (Roswell et al., 2019).

Females construct, maintain and defend their nests besides collecting pollen to provision young while males primarily search for suitable mates (Willmer & Stone, 2004).

Therefore, both may differ in their foraging and pollination efficiencies (Neeman et al., 2006). Female solitary bees usually forage more efficiently and consequently pollinate better than males (O'Toole & Raw, 1991). Males solitary bees however, contribute more to long-distance pollen flow (Neeman, et al., 2006).

According to recent studies, fruit set -in terms of quantitative and qualitative parameters including post-harvest characteristics- is more important predictor of pollination efficiency than pollen deposition (Wang et al., 2017). This is due to certain pollination limitations e.g. each stigma attains an asymptote after certain number of pollen grains (Sorensen & Webber, 1997), ovules attract pollen grains regardless of whether they are pre-pollinated or not (Falque et al., 1995) and deposition of non-viable and heterospecific pollen grains (Bellusci et al., 2020).

Since male and female solitary bees vary in foraging behavior and morphology, both are likely to deposit pollen grains in different ways. Females solitary bees are likely to deposit more viable pollen grains as they can exploit anthesis timing better and have shorter foraging distance and high visitation frequency than males (Neeman et al., 2006). Similarly, the amount of heterospecific pollen grains deposited on stigma by both the sexes may also vary as both show marked niche breadth and niche overlap in foraging resources (Roswell et al., 2019). Several species of Megachile (Latreille, 1802) (Hymenoptera: Megachilidae) bees have been reported as efficient crop pollinators in Indian subcontinents including *Mgegachile cephalotes* (Abrol et al., 2017a; Singh et al., 2017). The females of *M. cephalotes* have unbranched and spirally grooved hairs (scopa) on their abdominal sternum which make them morphologically efficient pollinator than the males (Kumar, 2015).

The present study aimed to investigate the foraging behavior of male and female *M. cephalotes* on phalsa crop, and how efficiently they pollinate phalsa plants in terms of pollen deposition, fruit setting and post-harvest characters. The effect of different environmental factors (light intensity, temperature, relative humidity and wind velocity) on foraging behavior was also studied.

Materials and methods

Study site and plant species:

The study was conducted at the Horticultural Research Farm of the University College of Agriculture and Environmental Sciences, Baghdad-ul-Jadeed Campus, The Islamia University of Bahawalpur (IUB), Punjab, Pakistan (29° 22' 36.59"N 71° 45' 44.04"E; 181 meters above sea level). The climate of the region is classified as subtropical with hot summers and cold winters. The mean daily minimum and maximum temperature reach 15°C and 30°C, in winter, and 20°C and 35°C, in summer, respectively. The average annual rainfall is 400 mm (PARC, 1980).

The experimental plant species was phalsa, *Grewia asiatica* L. (Malvaceae) sown in an area of 0.2 hectares containing 53 individuals. The nearby places include a planted forest, some waste land and buildings. Phalsa is a fruit bearing shrub (can grow up to 12 feet) native to Central America but is planted on commercial basis in Pakistan (Ullah et al., 2012; Singh et al., 2015). Yellow flowers (two centimeters in length) are borne in densely crowded axillary cymes. Fresh and dry fruits of phalsa are consumed in human diet and leaves are used as forage for livestock (Dev et al., 2017). In the Indian subcontinent, phalsa individuals bloom in February and the fruits ripen during April to June (Kumar et al., 2014). Phalsa is self-compatible but cross-pollination by insects can significantly improve the reproductive success (Randhawa & Dass, 1962). The study was conducted from mid-February to end-May 2018 (i.e. from flowering to harvesting).

Flower visitor censuses and foraging behavior

First, we conducted a three days-long survey of floral visitors in three widely isolated (>8 km) orchards (Table 3) in order to assess the pollinators profile of *G. asiatica* in Bahawalpur: Fisheries complex (29° 23' 15.4176'' N, 71° 37' 59.2284'' E), Lal-suhanra forest (29° 19' 2.2116'' N, 71° 54' 16.9056'' E) and IUB campus (29° 22' 36.588'' N, 71° 45' 44.0424'' E). One collector was deployed to collect floral visitors randomly using a hand collection net for 4 hours (8-9 am, 10-11 am, 4-5 pm and 6-7 pm local time) in each orchard. In this way the total sampling efforts were 12 hours in all the three orchards. The collected pollinators - other than *M. cephalotes* - were identified to family level by using taxonomic keys proposed by Borror et al. (1981). The body and proboscis length of both the female and male *M. cephalotes* was measured with a Vernier caliper (n= 15 each sex).

We only focused *M. cephalotes* for further studies at IUB campus: visitation frequency (number of bees visiting an inflorescence of casually 30 flowers during two minutes; n=40 in each census), visitation rate (number of flowers visited by an individual during 120 seconds; n=40 bee individuals in each census) and stay time (time spent in handling a flower by an individual during a visit; n=120 in each census) throughout the flowering season with weekly intervals (total 6 census). A stop watch was used to record these observations. During each census, observations were made at 10:00, 12:00, 14:00, and 16:00 hours along the day. Data regarding environmental factors such as temperature, relative humidity, wind speed and light intensity were recorded before each census with the help of thermo-hygrometer, anemometer and lux meter, respectively.

Pollinator effectiveness

Pollinator effectiveness was estimated in terms of pollen deposition, quantified after single visits of *M. cephalotes* on previously bagged flowers of *G. asiatica.* When *M. cephalotes* was abundant on the plants, the flowers were made available

to receive single visits. Once a flower has been visited by a female or a male bee, stigma was removed using a sharp blade. A stereoscopic microscope with 40× magnification was used to count pollen grains. Twenty such observations were made for each female and male *M. cephalotes* on twenty different plants in four splits i.e. five observations in each consecutive day for each sex.

To test the pollination efficiency of female and male *M. cephalotes* in terms of plant reproductive success, other floral buds were caged with nylon mesh bags 24 hours before they opened. They were un-caged during the peak activity time of *M. cephalotes* and re-caged once a single visit had been made by male or female bee. Ten such flowers on ten different plants were observed each for female and male *M. cephalotes*. The resultant fruit set and weight was measured as a function of their pollination efficiency. Twenty open-pollinated (unrestricted insect visitation) flowers and twenty caged (no insect visitation) flowers were also maintained on twenty different plants.

Post-harvest Qualities

The resulting fruits were harvested just at the start of ripening (i.e. 34 days after pollination) when their color was light pink. Harvested fruits were weighed using an electronic-balance with 6 hours of post-harvest interval until 78 hours. Since phalsa is a highly perishable fruit, the qualitative parameters including change in shape and color were also recorded at 6 hours of interval for 78 hours. The change in shape was recorded by visually attributing five ranks from tight skin to completely wrinkled skin. The change in color was carefully recorded using an RBG color chart i.e. ranged from deep pink to violet ret.

Data Analysis

In order to compare visitation frequency, visitation rate, stay time, pollen deposition, body length and proboscis length of male and female bees, the data were subjected to Man-Whitney U test (alpha 0.05) as it followed non-normal distribution. One-way ANOVA was applied to see the significant difference between average fruit weight of male, female and open pollinated fruits followed by Tukey's post hoc test at alpha 0.05. One-way ANOVA was also applied to see the significant difference between postharvest fruit weight loss (%) of male, female and open pollinated fruits at each observation hour (alpha 0.05). We did not include self-pollination in the analysis as all the fruits were aborted in self-pollination treatment.

Chi-square test was used to verify whether fruit wrinkling and color significantly changed over observation dates. In order to know how much the variation in foraging behavior (i.e. stay time, visitation rate and visitation frequency) of female and male *M. cephalotes* is explained by environment factors (temperature, relative humidity, wind speed and light intensity), multiple linear regression analysis was performed. The linear regression's F-test was applied with null hypothesis that model explains zero variance in dependent variables (foraging behavior). In order to see the significant environmental predictors of foraging behavior, their regression coefficients were compared at alpha 0.05 by using t-statistics.

Results

A total of 458 individuals belonging to 18 species in three orders visited the flowers of *G. asiatica* i.e. 13 bees (Hymenoptera), 2 butterflies, 1 moth (Lepidoptera) and 2 flies (Diptera). *Megachile cephalotes* comprised 65% of the total floral visitors' abundance on *G. asiatica* at all the three widely isolated locations in Bahawalpur i.e. fisheries complex, Lal-suhanra forest and IUB campus. This highlights the importance of *M. cephalotes* as a most frequent floral visitor of *G. asiatica* in Bahawalpur (Table 1).

Table 1. Relative abundance of *M. cephalotes* with other floral visitors at three widely isolated locations in Bahawalpur.

Locations	Total pollinator abundance	*M. cephalotes* Abundance	Percent *M. cephalotes* abundance
Fisheries complex	21	11	52.38
Lal Suhanra forest	24	12	50.00
IUB campus	458	300	65.50

The comparison of foraging behavior and morphological features of male and female *M. cephalotes* is presented in Table 2. There was no significant difference between male and female *M. cephalotes* in terms of stay time. However, visitation frequency, visitation rate and pollen deposition (2.06±0.14 individuals per branch per 2 minutes; 13.70±0.50 flowers per 2 minutes; 639.35±3.17 pollen grains per stigma, respectively) of females were significantly higher than that of males (0.44±0.06 individuals per branch per 120 seconds; 13.42±0.67 flowers per 2 minutes; 12.05±1.19 pollen grains per stigma, respectively). Regarding morphological features –important for cross pollination- female individuals had an edge over males by having longer body and proboscis lengths i.e. body length of 13.01±0.16 mm and 10.13±0.10 mm for female and male; proboscis length of 5.36±0.09 mm and 4.38±0.06 mm for female and male.

The results of multiple linear regression revealed that the models had very low values of R^2 and therefore did not explain much of the variation in foraging behavior (stay time, visitation frequency and visitation rate) on account of environmental factors however, they were significant (F-test; $p<0.001$) except the visitation frequency of male *M. cephalotes* (Table 3). The t-statistics showed that visitation frequency of both the sexes largely remained unaffected with environmental factors except for light intensity which was

Table 2. Comparison of foraging behavior and morphological features of female and male *M. cephalotes* using Man-Whitney U test at alpha 0.05 (n = number of observations**).**

Results of Man-Whitney U test	Foraging behavior				Morphological features	
	Stay time n = 360	Visitation rate n = 120	Visitation frequency n = 120	Pollen deposition n = 20	Body length n = 15	Proboscis length n = 5
Female (mean of ranks)	1777.21	71.6	200.61	15.03	11.5	4
Male (mean of ranks)	183.29	48.9	159.89	5.46	4	1.5
Mann-Whitney *U*	62609	4476	50141	8.5	0	0
p- value	0.431	<0.001	<0.001	<0.001	<0.001	0.007
Z-value	-0.78601	-5.1271	-5.2792	-5.1714	.-4.6455	.-2.5067

positively associated with the females. Wind significantly reduced the stay time in both the sexes while it improved the visitation rate in male bees. Light intensity reduced the stay time in males and improved the visitation rate in females. Temperature reduced the stay time in females and improved visitation rate of males (Table 3).

The activity of both the male and female *M. cephalotes* started somewhere between 9:00 am to 10:00 am. Males continued their activity in low abundance without any notable fluctuation across the observation intervals. However, females attained their peak abundance at 12:00 pm followed by a gradual decline until 4:00 pm (Fig 1).

Table 3. Multiple regression analysis between foraging behaviors of female and male *M. cephalotes* and environmental factors (M=male, F=female, T=temperature, R.H=relative humidity, W.S= wind speed, L.I=light intensity).

Gender		Model	F	P-value	R^2
Stay time	M	Y = 2.776 -0.047(T.) +0.149(R.H)* -0.058(W.S)* -0.005(L.I)*	17.516	<0.001	0.165
	F	Y= 15.513 -0.305(T.)* -0.045(R.H) -0.098(W.S)* -0.001(L.I)	8.530	<0.001	0.088
Visitation frequency	M	Y = -2.9 +0.0629(T.) +0.038 (R.H) -0.022(W.S) +0(L.I)	0.977	0.423	0.033
	F	Y= -0.991 +0.04(T.) -0.093 (R.H) -0.017(W.S) +0.007(L.I)*	6.815	<0.001	0.192
Visitation rate	M	Y= -37.557 +1.319(T.) -0.11 (R.H) +0.935(W.S)* +0.009(L.I)	6.237	<0.001	0.178
	F	Y = -57.76 +1.499(T.)* +0.293 (R.H) -0.056(W.S) +0.016(L.I)*	6.162	<0.001	0.177

*significant predictors of behavior using t-statistics at alpha 0.05

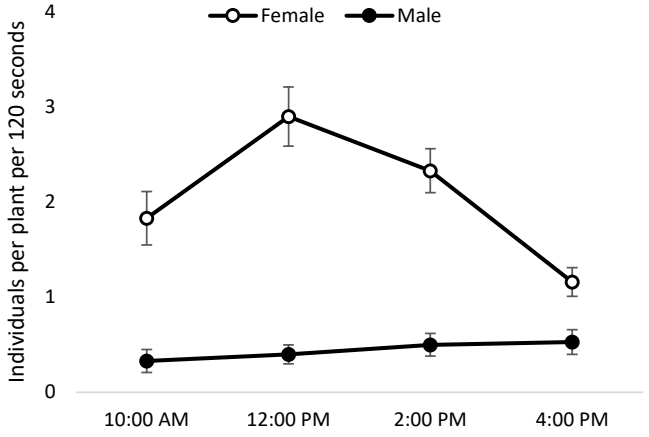

Fig 1. Diurnal dynamic pattern of Female and male *M. cephalotes* in terms of average individuals per plant per 120 seconds.

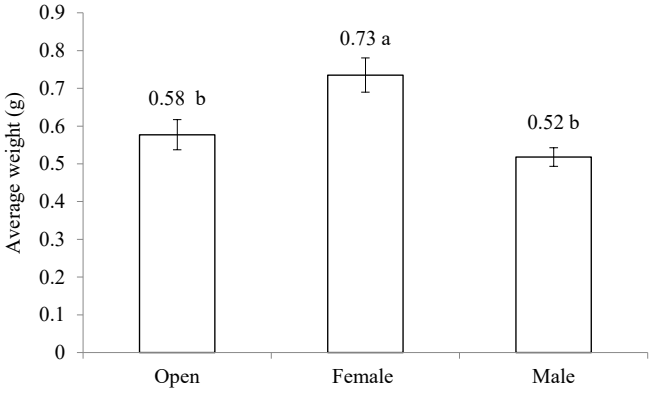

Fig 2. Comparison of female, male and open pollinated fruits in terms of their weight. Means sharing similar letters are statistically non-significant at alpha 0.05.

Open, female and male pollinated fruits were different in terms of their weight (d.f=2, f=8.84, p=0.001). The maximum average weight was recorded for female *M. cephalotes* pollinated fruits followed by open and male pollinated fruits which were also non-significant (Fig 2). Percent loss in weight was significantly lower in female pollinated fruits than that of open and male pollinated fruits at 6 hours after harvest (d.f. =2, p=0.012, f=5.20) and 12 (d.f. =2, p=0.001, f=9.82). Remaining observations from 18 to 78 h after harvest showed non-significant difference in weight loss.

The post-harvest decline in fruit weight was notably lower and more gradual in female pollinated fruits than open and male pollinated fruits. The fruits completely dried out at 54 h in case of open and male pollination whereas at 66 h in case of female pollination (Fig 3).

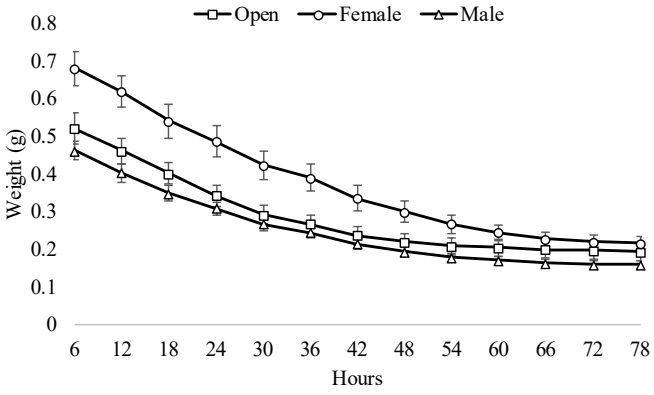

Fig 3. Fruit weight loss among open, female and male pollinated fruits after 6 to 78 hours of harvest.

In case of post-harvest wrinkling, as compared to male and open pollination, female pollinated fruits did not show any wrinkling until 18 h after harvest whilst overall wrinkling remained lower in female pollinated fruits than open and male pollinated fruits until 60 h. (Fig 4). Fruit wrinkling significantly increased ($p<0.001$) with the increase in post-harvest time in open pollinated, male pollinated and female pollinated fruits (χ^2=292, 325, 306, respectively) However, fruit color significantly changed ($p<0.001$) with the increase in post-harvest time in female pollinated fruits alone (χ^2=186).

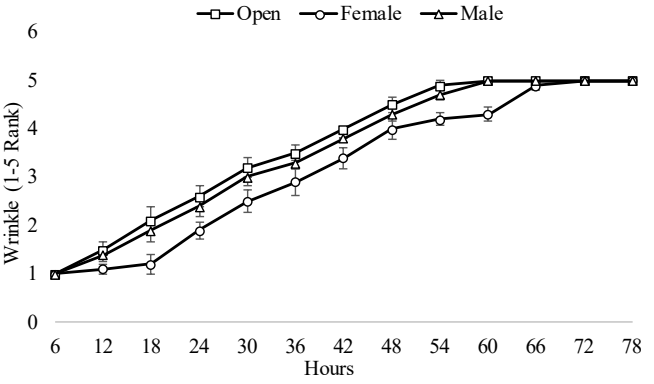

Fig 4. The increase in fruit wrinkling with successive post-harvest observation in case of open, female and male pollination

The result of survey of alternate host plants at IUB campus is shown in table 4. We observed 13 plant species which received at least one visit of male or female *M. cephalotes*. The maximum visits were recorded on *Alhagi graecorum* (Fabaceae).

Discussion

In this study we have shown that *M. cephalotes* was the most abundant (65% of total abundance of 18 species) floral visitor of *G. asiatica* in the study sites whilst its females were the more frequent and efficient pollinators. Phalsa flowers offer a rich source of energy and attract several pollinator populations e.g. including most abundant *Megachile, Apis* and *Xylocopa* species (Abrol, 1992). Kumar et al. (2017) also recorded 21 flower visitors on phalsa in India. *Grewia asciatica* therefore, shows a generalized pollination system (Ollerton et al., 2007) yet *M. cephalotes* being the most abundant visitor, might be leading the system towards cryptic specialization (Niemirski & Zych, 2011). In the present study, we, for the first time, gave the empirical evidence of how the male and female *M. cephalotes* - along with open and caged treatments - affect the qualitative parameters of phalsa, signifying female *M. cephalotes* as the best choice under local conditions.

Visitation frequency and pollen deposition of female bees was significantly higher than male bees in this study. Visitation frequency of male and female bees is the function of their relative abundance (i.e. proportion) in given space and time. The male-female ratio in *Megachile* bees is a highly variable phenomenon depending upon a number of physical factors e.g. size and diameter of nesting tunnel and distance of nest from foraging resource (Stephen & Osgood, 1965; Peterson & Roitberg, 2006). Moreover, females usually fly for shorter distances thereby increasing their visitation frequency and relative foraging efficiency while males contribute more to long-distance flow of pollen (Neeman, et al., 2006). Moreover, males in our study, foraged primarily on nectar and continued their activity in low abundance without any notable fluctuation across the observation intervals. Male solitary bees perform

Table 4. Visitation of *M. cephalotes* on alternate host plants at IUB campus.

Local names	Scientific names	No. of visits of *Megachile cephalotes*
Leh	*Cirsium arvense*	1
Maskeet	*Prosopis glandulosa*	3
Akk	*Calotropis procera*	1
Kindiari	*Carthamus persicus*	1
Ipleiple	*Leucaena leucocephala*	1
Parkinsonia	*Parkinsonia aculeata*	3
Janasa	*Alhagi graecorum*	9
Bukan	*Phyla nodiflora*	1
Alfalfa	*Medicago sativa*	4
Frash	*Tamarix aphylla*	2
Kikar	*Acacia nilotica*	1
Kheera	*Cucumis sativus*	3
Jand	*Prosopis cineraria*	2

at least two co-occurring activities i.e. nectar foraging and mate searching while females focus mainly on foraging for collecting pollen for their larvae (Neeman, et al., 2006). That is why males remained stable over day while females peaked at resource available time.

Pollen deposition in a single visit is predicted by a number of morphological and behavioral factors exhibited by bees. In *M. cephalotes*, females are larger in size than males besides having a number of scopal hairs on the ventral surface of their abdomen. This makes them a better pollen depositor than the males which are smaller in size with fewer scopal hairs (Bzdyk, 2012; Kumar, 2015). In the present study, female body length was in agreement with Kumar (2015) who reported female body length of 12.36-13.52 mm and male body length of 10.47-12.02 mm.

There was no significant difference between male and female *M. cephalotes* in terms of stay time. Female *M. cephalotes* is larger in size having longer proboscis than males. Moreover, females have to build nests, collect pollen for their young ones and lay eggs (Eickwort, 1975; Peterson & Roitberg, 2006). Therefore, to meet their energy and dietary requirements they have to uptake more nectar than the males (Feuerbacher et al., 2003). Previous studies have shown that bees with long proboscis ingest more volume of nectar than short proboscis (Harder, 1983). This suggests that no matter the stay time of both the sexes is similar, but female bees might ingest larger amount of nectar during a visit than the male did. Supporting this idea, Danforth (1990) reported that difference in food requirements between sexes starts right from the brood stage i.e. female offspring of *Calliopsis persimilis* (Megachilidae) receive three trips of pollen whereas male offspring receive two trips of pollen.

The comparison of male and female bees in their foraging response towards different environmental factors is rarely studied. In case of solitary bees '*M. lanata and M. bicolor'* - without giving the sex identity- Abrol and Kapil (1986) and Abrol (1987) found that visitation frequency was positively associated with light intensity, air temperature and solar radiation. In our case, visitation frequency of both the sexes of *M. cephalotes* largely remained unaffected with environmental factors except for light intensity which was positively associated with the females. This finding is in line with Szabo and Smith (1972) who also found a positive relationship between light intensity and visitation frequency of female *M. rotundata*.

How stay time and visitation rate of *Megachile* bees are affected by weather factors also remains unclear. Szabo and Smith (1972) showered that foraging activity of females *M. rotundata* was positively correlated with light intensity and temperature combined. In our study, wind speed significantly decreased the stay time in both the sexes while it improved the visitation rate in male bees. Similarly, light intensity negatively influenced the stay time in males and positively influenced visitation rate in females. Temperature negatively influenced the stay time in females and positively influenced the visitation rate of males. These findings are being reported for the first time for *M. cephalotes* and have implications for future studies and conservation programs.

Females in our study attained their peak abundance at 12:00 pm followed by a gradual decline until 4:00 pm. The activity of pollinators is mostly predicted by the anthesis, the time when large amount of nectar and pollen resources are available (Varassin et al., 2001). Kumar et al. (2017) noticed that anthesis lasted from 1130 to 1300 h in closely related *Grewia flavescens* in India. They also noticed the maximum pollen viability and stigmatic receptivity at the time of anthesis.

Results of present study showed females of *M. cephalotes* were the better pollinators than males. A single visit of females produced significantly greater fruit weight than that of male and open pollinated fruits, which were also statistically similar. Greater fruit weight in case of female *M. cephalotes* is certainly due to higher number of pollen grains deposited by them as compared to males. 'Why did the unrestricted open pollination result in lower fruit weight than the female *M. cephalotes* pollination?' can be justified in terms of pollen limitation. There are two pollination limitations associated with pollen grains i.e. quantity (number) and quality of pollen grains (Aizen & Harder, 2007). The seed set increases with the number of pollen grains deposited on stigma and attains an asymptote after certain number of pollen grains (Sorensen & Webber, 1997). The number of pollen grains dropped on stigma is not merely the indicator of good seed set as ovules attract pollen grains in the similar way regardless of whether they are pre-pollinated or not (Falque et al., 1995). Moreover, viability of pollen grains and number of heterospecific pollen grains also affect seed set in angiosperms (Bellusci et al., 2010).

Usually effective pollination has fortunate consequences on the post-harvested qualitative attributes like color, nutrient profile, size, firmness and overall shelf life of several fruits i.e. strawberry, feijoa, apples and almonds (Patterson, 1990; Brittain et al., 2014; Klatt et al., 2014a; Abrol et al., 2017b; Colak et al., 2017). These post-harvest qualities have strong link with the market value of fruits and economy of farmers (Klatt et al., 2014b).

Conclusion

Megachile cephalotes was the most abundant pollinator of phalsa in Bahawalpur. Females of *M. cephalotes* were the better pollinators than males in terms of pollen deposition, fruit weight, fruit size and shelf life (i.e. loss of fruit weight, shrinkage, and degradation in color). We also documented for the first time how abiotic factors including environment temperature, relative humidity, wind speed and light intensity affect the foraging behavior (stay time, visitation rate and frequency) of both female and male *M. cephalotes*.

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